

SPECIFICITY IN THE ASSOCIATION BETWEEN *HYDRACTINIA ECHINATA* AND SYMPATRIC SPECIES OF HERMIT CRABS¹

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Symbiotic associations between hermit crabs and cnidarians, particularly sea anemones, have been widely investigated. From his extensive behavioral and physiological studies of many hermit crab-sea anemone associations, Ross (1960, 1974) identified varying degrees of specificity, ranging from intimate obligatory relationships, e.g., that between *Pagurus prideauxi* and its "cloak anemone," *Adamsia palliata*; to non-obligatory, possibly chance associations. Since the work of Schijfsma (1935, 1939), the association between hermit crabs and the colonial hydrozoan, *Hydractinia echinata*, has received only limited attention.

Specimens of *Hydractinia echinata* form an encrusting, spinous, mat-like covering on their usual substrate, namely, gastropod shells. The occurrence of hydrozoans (e.g., *Hydractinia*) on hermit-crab-occupied shells influences the ecology and behavior of the host hermit crabs (Jensen, 1970; and Grant and Ulmer, 1974). In their studies of hermit crab populations from the Gulf of Mexico, Wright (1973), Conover (1976), Fotheringham (1976), and Mills (1976a) all discuss the differential occurrence of hydractiniids on shells occupied by *P. longicarpus*, *P. pollicaris*, and *Clibanarius vittatus*. Mills (1976a) states that smaller, common, sympatric hermit crab species (e.g., *P. annulipes*) "undoubtedly utilize some of the same shells as young individuals of the other three [larger] species," and that "the extent of their participation in the association has not been studied." Although Grant and Ulmer (1974) and Fotheringham (1976) have suggested that the association plays an important role in partitioning the gastropod shell resource, additional work is needed to substantiate and explain this.

Hermit crabs exhibit distinct behavior patterns in selecting shells (Reese, 1962, 1963). Most studies involving selection of shells have focused on the importance of such shell characteristics as species, morphology, weight, volume, aperture size, or a combination of these factors (Reese, 1962, 1963; Markham, 1968; Childress, 1972; Kuris and Brody, 1976; and Conover, 1978). Various aspects of shell availability and utilization as well as intra- and interspecific competition for suitable shells have been described by Orians and King (1964), Vance (1972a, b), Hazlett (1974), Kellogg (1976), Spight (1977) and Scully (1979). As recognized by Reese (1969), the shell functions as a microhabitat of the crab, and consequently, shell selection by hermit crabs should be regarded as a special form of habitat selection.

The purposes of this study were 1) to investigate the degree of specificity between species of hermit crabs and *Hydractinia*; 2) to determine the seasonality of

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the association; 3) to determine any pattern of specificity in shell-selection behavior of the sympatric hermit crabs *Pagurus annulipes*, *P. brevidactylus*, *P. longicarpus*, and *P. pollicaris*; and 4) to consider the occurrence of *Hydractinia* as a factor in the crabs' partitioning of the gastropod shell resource.

MATERIALS AND METHODS

Four to six samples were obtained each month from November, 1971, to February, 1973, from an area of Bogue Sound southwest of the Morehead City, North Carolina, port turning basin. Using a 1-m scallop dredge covered with 1/4-in mesh netting, collections from the oyster shell substrate were made at depths varying from 3 to 5 m after dredging for 15 min at a constant speed. From the contents of each dredge haul, all gastropod shells were collected and placed in buckets of sea water for later identification and analysis. For each sample, the numbers of unoccupied, snail-occupied, and hermit-crab-occupied shells were recorded. The species of shell and hermit crab also were identified. All shells were examined with a dissecting microscope for the presence of *Hydractinia* polyps.

Behavioral studies of three hermit crab species (*Pagurus annulipes*, *P. longicarpus*, and *P. pollicaris*) were conducted in the laboratory. All animals and shells were maintained in filtered sea water at 22°–24°C, 34–35‰ salinity, and under a 16-hr light: 8-hr dark photoperiod. Before testing, all crabs were removed from their shells and held separately in plastic divider-boxes for at least 1 week. Crabs were evicted by removing the shell apex with wire cutters and inserting a thin piece of wire that was wiggled until the crab vacated the shell. Only crabs possessing all appendages and free of obvious external parasites and injuries were used. Crabs were fed shrimp pellets for 1–2 hr on alternate days. The compartments were then cleaned and refilled with sea water.

Illynassa obsoleta shells, the most common shell species for all crab species, were maintained separately in sea water. The interior of each shell used was cleaned by repeated brushing with wire pipe cleaners and rinsing. The shell exteriors without *Hydractinia* colonies were cleaned by light brushing under flowing tap water. Only shells completely encrusted with a living mat of *Hydractinia* were used as *Hydractinia* shells (HS), and only those without the hydroid and free of other fouling organisms were used as plain shells (PS). The *Hydractinia* colonies were fed freshly hatched *Artemia* larvae for 1–2 hr on alternate days. Their compartments were then cleaned and refilled with sea water.

Due to a shortage of appropriate *Hydractinia*-covered shells and the scarcity of the hermit crab *P. brevidactylus*, this species was not included in the laboratory studies. (While this report was in press we learned of a paper by McLaughlin, 1975, which indicates that the crab identified in our report as *Pagurus brevidactylus* has been described as a new species, *Pagurus carolinensis*.)

Considerable evidence (Reese, 1962, 1963; Vance, 1972a; Kellogg, 1976) indicates that hermit crabs exhibit shell-size specificity. From his extensive studies on shell utilization by hermit crabs, including the species in this study, Kellogg (1971) has shown that the length of the anterior shield (ASL) of the hermit crab carapace is a reliable measure of crab size. The anterior-shield length (the distance from the top of the rostrum to the midpoint of the cervical suture) was measured (± 0.01 mm) with a dissecting microscope fitted with an ocular micrometer. Kellogg (1971) also indicated that shell width and shell weight were reliable measures of shell size. We froze specimens of *P. annulipes*, *P. longicarpus*,

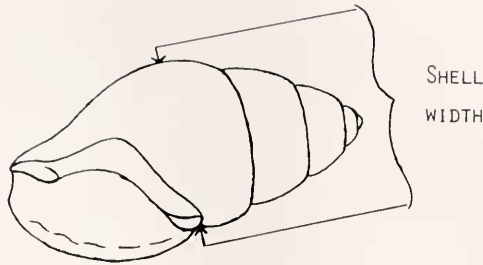


FIGURE 1. Shell width (SW) measurement of gastropod shell size.

and *P. pollicaris* occupying *I. obsoleta* shells that were not fouled, damaged, or covered with *Hydractinia*. Upon thawing, the crabs were easily extracted intact, and ASL measurements were made. Shell widths and shell weights (wet) were obtained for each vacated shell. Between 14 and 30 observations were made for each of the three crab species. The relationships between ASL-shell width and ASL-shell weight were established by standard regression methods. For all three crab species, shell width accounted for more of the variation in crab size than did shell weight. Therefore, shell width (SW) was selected as the primary variate of interest and used in matching suitably sized shells to crabs to be tested. The equations describing the SW-ASL relationship for each crab species are: for *P. annulipes*, $SW = 4.815 + 1.602 (ASL)$, for *P. longicarpus*, $SW = 1.486 + 2.836 (ASL)$; and for *P. pollicaris*, $SW = 5.812 + 1.545 (ASL)$.

Shell width (SW) was defined as the distance between the juncture of the outer lip and first suture on one side of the shell and the point first contacted by calipers on the body whorl directly opposite (Fig. 1). This measurement was always made perpendicular to the longitudinal axis of the shell, *i.e.*, from the shell apex to the aperture of the anterior siphonal canal. Shell width measurements were with vernier calipers graduated in 0.1 mm and read with the aid of a dissecting microscope.

The shell-selection experiments were conducted in an illuminated test chamber where thirty 150-ml culture dishes each containing 100 ml of filtered sea water, were arranged in five rows of six dishes each. With the remainder of the room in darkness, the crabs could be observed through viewing ports with little risk of disturbing them. Into each of these dishes containing 100 ml of filtered sea water a naked (without a shell) hermit crab of known size was placed. Two crabs of each species were randomly selected and assigned within each row. Empty gastropod shells were added after 24 hrs acclimation.

In Experiment I (HS *vs.* PS) 30 individuals of each crab species were tested for preference for *Hydractinia* shells (HS) or plain shells (PS). For each crab, a pair of *I. obsoleta* shells, one covered with a *Hydractinia* colony and one without, was selected according to the shell width (SW) appropriate for the ASL of the crab. Attempts were made to match the shells as closely as possible regarding SW (± 0.05 mm), color, and condition, so that the only noticeable difference between the matched shells would be the presence or absence of a colony of *Hydractinia*. Shells were matched to within ± 0.3 mm of the expected acceptable shell size for the crab to be tested. The paired shells were added simultaneously to each dish in a row within the test chamber. The shell occupied after 24 hr was considered the "preferred" shell.

TABLE I

*Hermit crab abundance and the utilization of Hydractinia-shells: HS = shells with Hydractinia, and PS = shells without Hydractinia. *Based on the overall occurrence of Hydractinia-covered shells in the total hermit crab population.*

| Hermit crab species | % of total | PS | HS | % HS | χ^2 | P^* |
|-----------------------------|------------|------|-----|------|----------|--------|
| <i>Pagurus longicarpus</i> | 36.2 | 700 | 288 | 29.1 | 48.8 | <0.001 |
| <i>P. annulipes</i> | 28.7 | 780 | 3 | 0.4 | 191.0 | <0.001 |
| <i>P. pollicaris</i> | 18.6 | 257 | 251 | 49.4 | 268.4 | <0.001 |
| <i>P. brevidactylus</i> | 14.6 | 397 | 3 | 0.8 | 94.0 | <0.001 |
| <i>Paguristes hummi</i> | 1.2 | 30 | 2 | 13.7 | 1.4 | >0.100 |
| <i>Clibanarius vittatus</i> | 0.4 | 8 | 2 | | | |
| <i>Petrochirus diogenes</i> | 0.3 | 5 | 3 | | | |
| <i>Paguristes tortugae</i> | <0.1 | 1 | 0 | | | |
| Total | | 2178 | 552 | 20.2 | | |

In Experiment II (DS vs. PS), the same criteria for shell pairing and matching to crabs were employed as in Experiment I. However, shells covered with the perisarcal crust of a dead *Hydractinia* colony (DS) were substituted for shells covered with a living hydroid colony. No crabs used in Experiment I were retested in Experiment II. The observations on each species of crab were made in the same manner as described for Experiment I.

To indicate the degree of "rejection" of shells not chosen in Experiments I and II, a second pair of experiments was conducted. Experiment III was conducted to determine if crabs that rejected HS shells in Experiment I would accept a *Hydractinia* shell when given no other shell to enter. Experiment IV tested whether crabs that rejected a perisarc shell (DS) in Experiment II would accept such a shell when given no other to enter. In these experiments crabs that chose a PS shell in Experiments I or II were evicted and returned naked to culture dishes containing new sea water. After a 24-hr acclimation period, the crabs from Experiment I were retested given only the original HS shell to enter. Similarly, in Experiment IV crabs that rejected a DS shell were given only the original DS shell to enter.

RESULTS

Utilization of gastropod shells by hermit crabs

Eight species of hermit crabs occupied 46% of all gastropod shells collected from Bogue Sound. Of the remaining shells, 32% were unoccupied (*i.e.*, did not contain a hermit crab or snail), and 22% housed a living snail. The four most common species of hermit crabs were *Pagurus annulipes*, *P. brevidactylus*, *P. longicarpus*, and *P. pollicaris*, which together comprised over 98% of the 2730 individuals obtained (Table I).

Twenty-three species of gastropod shells were recorded from the total of 5885 shells collected in 78 dredge hauls, with 10 species comprising over 96% of the shells (Table II). Only six shell species, however, were inhabited by all four common crab species. Each of these shell species (*Eupleura caudata*, *Fasciolaria hunterii*, *I. obsoleta*, *Nassarius vibex*, *Terebra dislocata*, and *Urosalpinx*

TABLE II

Shell utilization and the occurrence of *Hydractinia* on common shell species occupied by hermit crabs. PS = shells without *Hydractinia*. HS = shells with *Hydractinia*.

| Shell species | <i>P. annulipes</i> | | | <i>P. brevidactylus</i> | | | <i>P. longicarpus</i> | | | <i>P. pollicaris</i> | | |
|-----------------------------|---------------------|----|------|-------------------------|----|------|-----------------------|-----|------|----------------------|-----|-------|
| | PS | HS | % HS | PS | HS | % HS | PS | HS | % HS | PS | HS | % HS |
| <i>Anachis</i> spp. | 36 | 0 | 0.0 | 7 | 0 | 0.0 | — | — | — | — | — | — |
| <i>Busycon</i> spp. | — | — | — | 1 | 0 | 0.0 | 3 | 0 | 0.0 | 58 | 49 | 35.8 |
| <i>Eupleura caudata</i> | 42 | 0 | 0.0 | 16 | 0 | 0.0 | 9 | 1 | 10.0 | 3 | 0 | 0.0 |
| <i>Fasciolaria hunterii</i> | 3 | 0 | 0.0 | 2 | 0 | 0.0 | 10 | 6 | 37.5 | 34 | 46 | 57.5 |
| <i>Ilyanassa obsoleta</i> | 337 | 1 | 0.3 | 241 | 1 | 0.4 | 483 | 223 | 31.6 | 87 | 71 | 44.9 |
| <i>Littorina irrorata</i> | — | — | — | — | — | — | 18 | 10 | 35.7 | 3 | 6 | 66.7 |
| <i>Nassarius vibex</i> | 242 | 2 | 0.8 | 55 | 2 | 3.6 | 106 | 27 | 20.3 | 7 | 1 | 12.5 |
| <i>Polinices duplicatus</i> | — | — | — | — | — | — | 14 | 6 | 30.0 | 36 | 66 | 64.7 |
| <i>Terebra dislocata</i> | 31 | 0 | 0.0 | 6 | 0 | 0.0 | 6 | 1 | 14.3 | 0 | 1 | 100.0 |
| <i>Urosalpinx cinerea</i> | 77 | 0 | 0.0 | 65 | 0 | 0.0 | 24 | 12 | 33.3 | 17 | 4 | 19.1 |
| Other | 12 | 0 | 0.0 | 4 | 0 | 0.0 | 21 | 2 | 8.7 | 12 | 7 | 36.8 |
| Total | 780 | 3 | 0.4 | 397 | 3 | 0.8 | 700 | 288 | 29.1 | 257 | 251 | 49.4 |

cinerea) also supported colonies of *Hydractinia* and, in total, constituted 86% of the shells occupied by hermit crabs.

Even though many shell species were available, one species, *I. obsoleta*, was most frequently utilized by all common hermit crab species in Bogue Sound (Table II). *P. annulipes* primarily inhabited *I. obsoleta* (43.2%) and *Nassarius vibex* (31.2%) shells, whereas *P. brevidactylus* mostly inhabited *I. obsoleta* (60.5%) and *Urosalpinx cinerea* (16.2%) shells. Although *P. longicarpus* inhabited the greatest variety of shell species, it was also primarily found in *I. obsoleta* shells (71.5%). The greatest number of *P. pollicaris* (31.1%) were collected in *I. obsoleta* shells. Larger members of this species, however, were frequently collected in two species of *Busycon*, *Fasciolaria hunterii*, and *Polinices duplicatus* shells.

Occurrence of *Hydractinia* on hermit crab-occupied shells

Nearly all of the *Hydractinia*-colonized shells (98%) were occupied by hermit crabs. The remaining colonized shells were found unoccupied. Chi-square contingency table analysis indicated significant differences in the incidence of *Hydractinia* on shells occupied by different crab species. Since *Hydractinia* colonized 20% of all hermit-crab-occupied shells, it would be expected that approximately 20% of each crab species would occupy a *Hydractinia* shell (Table I) if the association were independent of species. The percentages of *Hydractinia* shells occupied by *P. annulipes* (0.4%) and *P. brevidactylus* (0.8%) were less than expected ($P < 0.001$) while the percentages of *Hydractinia* shells occupied by *P. longicarpus* (29%) and *P. pollicaris* (49%) were greater than expected ($P < 0.001$). In addition, the occurrence of the hydroid with *P. annulipes* was not significantly different ($P < 0.50$) from that with *P. brevidactylus*, while its occurrence with *P. longicarpus* and *P. pollicaris* was significantly different between these species as well as between these and the other two species ($P < 0.001$).

If the occurrence of *Hydractinia* were related to shell species and not to hermit crab species, then the hydroid would be present only on certain shell species without regard to the species of crab inhabiting the shell. Therefore, we compared the occurrence of *Hydractinia* on the six shell species occupied by all four hermit crab species (Tables II, III). The hydroid was found on all six shell species; but more

TABLE III

Occurrence of *Hydractinia* on shells occupied by four species of hermit crabs from Bogue Sound: PS = shells without *Hydractinia*, and HS = shells with *Hydractinia*. * Based on the occurrence of HS shells occupied by the total hermit crab population as indicated in each section of the table.

| Hermit crabs | PS | HS | % HS | χ^2 | P* |
|--|------|-----|------|----------|--------|
| Pooled results of the six shell species inhabited by all four common hermit crab species | | | | | |
| <i>P. annulipes</i> | 732 | 3 | 0.4 | 146.9 | <0.001 |
| <i>P. brevidactylus</i> | 385 | 3 | 0.8 | 74.3 | <0.001 |
| <i>P. longicarpus</i> | 638 | 270 | 29.7 | 97.4 | <0.001 |
| <i>P. pollicaris</i> | 148 | 123 | 45.4 | 148.7 | <0.001 |
| Total | 1903 | 399 | 17.3 | 467.4 | <0.001 |
| Same as above but excluding <i>Ilyanassa obsoleta</i> shells | | | | | |
| <i>P. annulipes</i> | 395 | 2 | 0.5 | 49.8 | <0.001 |
| <i>P. brevidactylus</i> | 144 | 2 | 1.4 | 15.6 | <0.001 |
| <i>P. longicarpus</i> | 155 | 47 | 23.3 | 24.4 | <0.001 |
| <i>P. pollicaris</i> | 61 | 52 | 46.0 | 123.2 | <0.001 |
| Total | 755 | 103 | 12.0 | 213.0 | <0.001 |
| Occurrence of <i>Hydractinia</i> on <i>I. obsoleta</i> shells only | | | | | |
| <i>P. annulipes</i> | 387 | 1 | 0.3 | 82.6 | <0.001 |
| <i>P. brevidactylus</i> | 241 | 1 | 0.4 | 58.5 | <0.001 |
| <i>P. longicarpus</i> | 483 | 223 | 31.6 | 57.7 | <0.001 |
| <i>P. pollicaris</i> | 87 | 71 | 44.9 | 60.5 | <0.001 |
| Total | 1148 | 296 | 20.5 | 264.9 | <0.001 |

frequently than expected ($P < 0.001$) on shells occupied by *P. longicarpus* and *P. pollicaris* and less frequently than expected ($P < 0.001$) on shells occupied by *P. annulipes* and *P. brevidactylus* (Table III). Also, *Hydractinia* occurred much more often on shells housing *P. pollicaris* and *P. longicarpus* ($P < 0.001$) than on shells occupied by other species. Its frequency on shells housing *P. annulipes* did not differ from its frequency on *P. brevidactylus* shells ($P < 0.70$).

Since one shell species, *I. obsoleta*, comprised over 54% of all hermit-crab-occupied shells, one might suspect that the pattern of association between hermit crab species and *Hydractinia* could result directly from the abundance of *I. obsoleta* shells. To resolve this question, we analyzed the frequency of *Hydractinia* on those shell species commonly occupied by all four crab species, excluding *I. obsoleta* from the pooled totals. Here again, *P. annulipes* and *P. brevidactylus* inhabited *Hydractinia* shells significantly less often ($P < 0.001$) than did *P. longicarpus* or *P. pollicaris* (Table III). Using contingency tables and Fisher's Exact Probability Test, an analysis of the occurrence of *Hydractinia* on *I. obsoleta* shells alone also showed the same pattern of hermit crab specificity (Table III).

The frequency with which each hermit crab species inhabited *Hydractinia* shells was calculated for each monthly collection to determine seasonal differences. In all monthly collections, *Hydractinia* was rarely found on shells occupied by *P.*

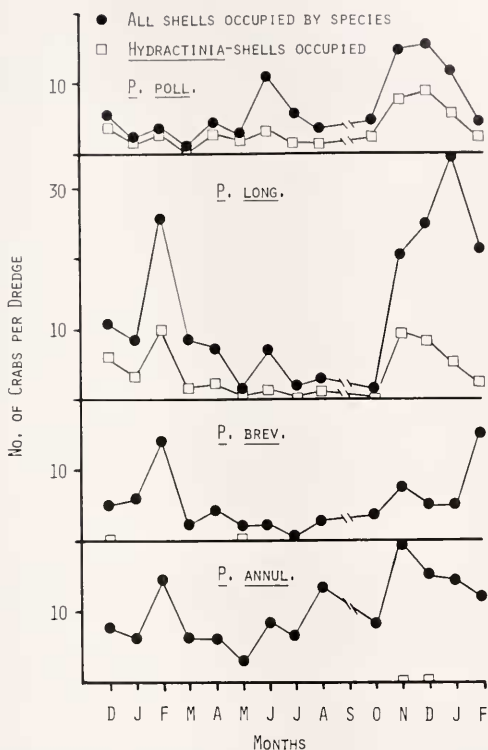


FIGURE 2. Seasonal abundance of *Hydractinia* and species of hermit crabs from Bogue Sound, *P. annul.* = *Pagurus annulipes*, *P. brev.* = *P. brevidactylus*, *P. long.* = *P. longicarpus*, *P. poll.* = *P. pollicaris*.

annulipes or *P. brevidactylus* but was frequently found on shells inhabited by *P. longicarpus* and *P. pollicaris*.

Hermit crabs and *Hydractinia* shells were more abundant from November through February than from March through October (Fig. 2). From November, 1972, to February, 1973, numbers of hermit crabs increased markedly with *P. longicarpus* showing the greatest increase. Concurrent increases in *Hydractinia* shells occupied by *P. longicarpus* and *P. pollicaris* occurred during these months; however, no appreciable increase was evident in *Hydractinia* shells occupied by *P. annulipes* or *P. brevidactylus*.

Shell-selection experiments

Two types of experiments were conducted to determine whether each hermit crab species exhibited shell preference behavior relating to the presence of *Hydractinia* or the perisarcular remains of a dead *Hydractinia* colony. Experiments I and II ("two-choice" experiments) showed that shell preferences exist, while experiments III and IV ("single-choice" experiments) indicated the degree of rejection of a hydroid-covered or perisarc-covered shell.

Experiment I: Hydractinia shell (HS) vs. plain shell (PS). In this experiment *P. annulipes* and *P. longicarpus* rejected HS shells more often than expected on the basis of chance and *P. pollicaris* accepted HS shells more often than expected

TABLE IV
Shell selection experiments.

| Two-choice experiments (Random shell selection expected) | | | | | Single-choice experiments (100% shell selection expected) | | | |
|---|----------|----|----------|--------|--|----|----------|--------|
| Hermit Crabs | HS or DS | PS | χ^2 | P | HS or DS | NS | χ^2 | P |
| I. <i>Hydractinia</i> shell (HS) vs. plain shell (PS) | | | | | III. <i>Hydractinia</i> shell (HS) vs. no shell (NS) | | | |
| <i>P. annulipes</i> | 2 | 28 | 22.5 | <0.001 | 14 | 13 | 12.5 | <0.001 |
| <i>P. longicarpus</i> | 8 | 22 | 6.5 | <0.05 | 22 | 0 | 0 | — |
| <i>P. pollicaris</i> | 23 | 7 | 8.5 | <0.005 | 7 | 0 | 0 | — |
| II. Perisarc shell (DS) vs. plain shell (PS) | | | | | IV. Perisarc shell (DS) vs. no shell (NS) | | | |
| <i>P. annulipes</i> | 8 | 12 | 0.8 | >0.05 | 11 | 0 | — | — |
| <i>P. longicarpus</i> | 9 | 11 | 0.2 | >0.05 | 11 | 0 | — | — |
| <i>P. pollicaris</i> | 13 | 6 | 2.6 | >0.05 | 3 | 0 | — | — |

(Table IV). Only 2 of 30 *P. annulipes* (7%) chose *Hydractinia*-covered shells (HS) after 24 hr. According to the chi-square test, this result is significantly different from random ($P < 0.001$). Twenty-three of 30 (77%) *P. pollicaris*, on the other hand, chose HS shells ($P < 0.005$). Eight of 30 *P. longicarpus* chose HS shells. This result was significantly different from the expected random selection ($P < 0.05$).

Experiment II: Perisarc shell (DS) vs. plain shell (PS). Experiment II paired shells with only the spinous perisarc crust remaining from a dead *Hydractinia* colony (DS) with plain shells (PS). Random shell-selection behavior was exhibited by all three crab species tested in this experiment. Thus, the selection of DS shells as opposed to PS shells by *P. annulipes*, *P. longicarpus*, and *P. pollicaris* was not significant (chi-square, $P > 0.05$). Although only 40% of the *P. annulipes* selected DS shells as compared to 68% of the *P. pollicaris*, this difference was not significant (adjusted chi-square, $P > 0.05$). DS shell selection by *P. longicarpus* also did not differ from that by *P. annulipes* or *P. pollicaris* ($P > 0.05$).

Experiment III: Hydractinia shell (HS) vs. no shell (NS). Those individuals rejecting HS shells in Experiment I were retested and exposed only to HS shells. After 24 hr in the test dishes, 13 of the 27 *P. annulipes* remained naked (i.e., without a shell), while 100% of the *P. longicarpus* and *P. pollicaris* entered the *Hydractinia* shell (Table IV). Thus, 48% of the *P. annulipes* did not enter a HS shell, even though it was the only shell available. According to Fisher's Exact Probability Test, HS selection by *P. annulipes* differed significantly from *P. longicarpus* and *P. pollicaris* ($P < 0.02$).

Experiment IV: Perisarc shells (DS) vs. no shell (NS). All crabs tested in this "single-choice" experiment entered the DS shells rather than remain without a shell (Table IV). Therefore, the DS shells did not elicit shell rejection behavior by *P. annulipes* as did the HS shells.

Ten crabs used in shell selection experiments I and II were treated for 24 hr prior to testing in a sea water solution containing 25 ppb $HgCl_2$, to determine if sublethal levels of $HgCl_2$ would alter shell selection behavior. The results indicated no significant difference in the selection of HS or DS shells by

crabs dosed with HgCl_2 and untreated controls. Fisher's Exact Probability Test was used to determine homogeneity of this data. Since the results for all three hermit crab species showed no significant difference between treated and control animals, these data were pooled.

DISCUSSION

The presence of *Hydractinia* on hermit-crab-occupied shells is clearly not random in Bogue Sound, N. C. The frequency of *Hydractinia*-colonized shells occupied by *P. annulipes* and *P. brevidactylus* was less than 1%, while the frequencies of such shells housing *P. longicarpus* and *P. pollicaris* were 29% and 49%, respectively. This pattern of specificity was significantly different from the expected 20%, the frequency of *Hydractinia* for the total hermit crab population.

Field studies from different areas support the concept of non-random occurrence of hydractiniid hydrozoans on hermit-crab-occupied gastropod shells. Grant and Ulmer (1974) showed that *P. adrianus* inhabits *Hydractinia* shells more frequently than *P. pubescens* in the Frenchman Bay area of Maine. Wright (1973) found that *P. longicarpus* and *P. pollicaris* in Galveston Bay, Texas, often occur in shells supporting either *Hydractinia* or *Podocoryne carnea*, while *Clibanarius vittatus* was rarely observed in shells with hydroids. In other studies of Gulf Coast hermit crabs, Mills (1976a, b) reported 71% of specimens of *P. pollicaris* and 30% of *P. longicarpus* with either *Hydractinia* or *Podocoryne scelna*, and Fotheringham (1976) observed the same two crab species utilizing hydroid-covered shells with a frequency of 62% and 30% respectively. Both of the latter authors found hydractiniid colonies absent or rare on shells occupied by *C. vittatus*. Neither reports any data on *P. annulipes*. We have rarely seen *C. vittatus* in a *Hydractinia*-covered shell along the North Carolina coast.

It is well established that certain species of hermit crabs exhibit clear preferences for the shells of certain gastropod species (Reese, 1962, 1963; Orians and King, 1964; Markham, 1968; and Hazlett, 1971). It has also been suggested that *Hydractinia* frequently colonizes the same species of shells most often occupied by certain crab species (Crowell, 1945). Thus, we must ask whether hermit crabs are selecting for *Hydractinia* or for shell species. If the species of shell were the major factor influencing the association, then certain species of shells commonly occupied by each crab species, especially *P. longicarpus* and *P. pollicaris*, should not be found supporting *Hydractinia* colonies. However, our data shows that those shell species commonly occupied by all four hermit crab species (except *E. caudata*) frequently supported colonies of the hydroid when occupied by *P. longicarpus* and *P. pollicaris*. Conversely, the same shell species rarely supported *Hydractinia* when occupied by *P. annulipes* or *P. brevidactylus*. Similar results by Grant and Ulmer (1974) indicate that the species of shell colonized had little apparent effect on the preference for *Hydractinia* shells exhibited by *P. adrianus*. Their work also suggests that the presence of *Hydractinia* must be an important factor in the selection of shells by certain crab species.

Seasonal factors influence various aspects of the biology of hermit crabs (Reese, 1968; Samuelsen, 1970; and Fotheringham, 1975). The seasonal occurrence of hermit crabs in association with *Hydractinia*, however, has not previously been reported. In each of the monthly collections of this study, *Hydractinia* occurred most frequently on shells occupied by *P. longicarpus* or *P. pollicaris* and rarely on those occupied by *P. annulipes* or *P. brevidactylus*. The former two crab species

were most abundant from November through February, when the highest frequencies of *Hydractinia* shells were also found. Thus, the population densities of both *P. longicarpus* and *P. pollicaris* appear to have an important relationship with the abundance of the hydroid.

Various investigators (Jensen, 1970; Grant and Ulmer, 1974; and Conover, 1976) suggest that shell-selection behavior is influenced by the presence of *Hydractinia*. This suggestion is supported by the results of our shell preference studies where *P. annulipes* frequently rejected *Hydractinia* shells even when hydroid-covered shells were the only ones available. On the other hand, *P. longicarpus* and *P. pollicaris* readily accepted *Hydractinia* shells. The rejection of hydroid-covered shells even when no other shells were available was also reported by Wright (1973) for *C. vittatus*. A naked hermit crab that rejected a non-preferred shell in its natural environment would be more vulnerable to predation.

The encrusting mat of perisarc produced by *Hydractinia* gives the shell a rough-textured surface. It might be hypothesized that shell selection or rejection might be due to the crust rather than the living hydroid. Our laboratory experiment showed, however, that each species of hermit crab selected shells without regard to the presence of the perisarc crust. The living *Hydractinia* colony, therefore, and not the perisarc crust, appears to provide the stimulus for the differential selection of *Hydractinia* shells by various species of hermit crabs. This conclusion is in accord with the findings of Jensen (1970), who showed that *P. bernhardus* exhibited a clear preference for shells covered with living colonies of *Hydractinia*. We suggest that shell selection behavior of the crabs plays the primary role in determining the pattern of association between symbiotic hydractiniid hydroids and various hermit crab species.

Coexistence of sympatric species depends upon many factors. Vance (1972a) demonstrated that both resource and habitat partitioning are important mechanisms facilitating the coexistence of hermit crab species. The occurrence of *Hydractinia* on available gastropod shells may act as a resource partitioning mechanism, as suggested by Grant and Ulmer (1974) and Fotheringham (1976). Such a mechanism could reduce competition for shells among the sympatric species of hermit crabs from Bogue Sound, N. C.

From his studies of seven sympatric populations of hermit crabs from nearby Beaufort Harbor, N. C., Kellogg (1977) concludes that co-existence of these populations depends upon habitat differences, shell-size partitioning, and shell-species partitioning, in that order. His earlier report (Kellogg, 1976) suggests that the restricted abundance of shells of adequate size and condition may be a factor limiting the size of hermit crab populations, particularly those of the largest species (*P. pollicaris*). The three most abundant species in this area partition the shell resource according to size, with *P. annulipes* commonly occupying the smallest shells, *P. longicarpus* the intermediate, and *P. pollicaris* the largest sizes (Kellogg, 1977). This, however, does not preclude size overlap. In our studies, individuals of each species ranging in ASL size from 1.9 to 2.9 mm were commonly collected. Although smaller shells are more abundant, so are the numbers of species and individuals competing for these shells. Our findings indicate that one species of shell (*I. obsoleta*) is most frequently occupied by each crab species. Shells of this species were most likely not produced in the subtidal habitat of Bogue Sound, since few live gastropods were collected in this area (Mercando, 1975). These factors could only increase competition for shells of small or intermediate size. Since *P. pollicaris* indicates strong preferences for *Hydractinia* shells while *P. annulipes* and *P. brevidactylus*

do not, younger members of the former species effectively compete only with *P. longicarpus* for hydroid-covered shells. Therefore, in addition to shell-size selection, *Hydractinia*-shell selection behavior may act to further partition the gastropod shell resource from Bogue Sound.

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SUMMARY

1. A distinct pattern in the occurrence of *Hydractinia* on shells occupied by four sympatric species of hermit crabs was identified. *Hydractinia* occurred most frequently on shells occupied by *Pagurus longicarpus* and *P. pollicaris* and rarely on shells occupied by *P. annulipes* and *P. brevidactylus*. The abundance of *Hydractinia* fluctuated seasonally, concurrent with changes in the abundance of *P. longicarpus* and *P. pollicaris*.

2. Species of shell appeared to be a less significant factor than species of crab in determining the pattern of association between *Hydractinia* and hermit crabs.

3. In laboratory studies, naked *P. annulipes* rejected *Hydractinia*-covered shells even when offered only such shells to enter, while *P. longicarpus* and *P. pollicaris* readily accepted *Hydractinia*-covered shells. None of the three species showed any preference for or against shells supporting only the perisarcal crust of dead *Hydractinia* colonies.

4. Our results indicate that occurrence of *Hydractinia* on gastropod shells acts to partition this resource and thereby tends to reduce competition among the four sympatric species of hermit crab in Bogue Sound, N. C.

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